

SPECIAL FEATURE

GRASS-WOODLAND TRANSITIONS

An ecosystem services perspective on brush management: research priorities for competing land-use objectives

Steven R. Archer* and Katharine I. Predick

School of Natural Resources & The Environment, The University of Arizona, Tucson, AZ 85745-0043, USA

Summary

1. The vegetation of semi-arid and arid landscapes is often comprised of mixtures of herbaceous and woody vegetation. Since the early 1900s, shifts from herbaceous to woody plant dominance, termed woody plant encroachment and widely regarded as a state change, have occurred world-wide. This shift presents challenges to the conservation of grassland and savanna ecosystems and to animal production in commercial ranching systems and pastoral societies.

2. Dryland management focused on cattle and sheep grazing has historically attempted to reduce the abundance of encroaching woody vegetation (hereafter, 'brush management') with the intent of reversing declines in forage production, stream flow or groundwater recharge. Here, we assess the known and potential consequences of brush management actions, both positive and negative, on a broader suite of ecosystem services, the scientific challenges to quantifying these services and the trade-offs among them.

3. Our synthesis suggests that despite considerable investments accompanying the application of brush management practices, the recovery of key ecosystem services may be short-lived or absent. However, in the absence of such interventions, those and other ecosystem services may be compromised, and the persistence of grassland and savanna ecosystem types and their endemic plants and animals threatened. **4.** Addressing the challenges posed by woody plant encroachment will require integrated management systems using diverse theoretical principles to design the type, timing and spatial arrangement of initial management actions and follow-up treatments. These management activities will need to balance cultural traditions and preferences, socio-economic constraints and potentially competing land-use objectives.

5. *Synthesis.* Our ability to predict ecosystem responses to management aimed at recovering ecosystem services where grasslands and savannas have been invaded by native or exotic woody plants is limited for many attributes (e.g. primary production, land surface–atmosphere interactions, biodiversity conservation) and inconsistent for others (e.g. forage production, herbaceous diversity, water quality/quantity, soil erosion, carbon sequestration). The ecological community is challenged with generating robust information about the response of ecosystem services and their interactions if we are to position land managers and policymakers to make objective, science-based decisions regarding the many trade-offs and competing objectives for the conservation and dynamic management of grasslands and savannas.

Key-words: bush clearing, drylands, ecosystem services, shrub encroachment, state change, vegetation change, woody plant encroachment, woody weeds

Introduction

The vegetation of semi-arid and arid landscapes (hereafter 'drylands') is often comprised of varying mixtures of herbaceous and woody vegetation, and the abundance of these contrasting plant life forms is highly dynamic (Bond, Midgley & Woodward 2003). Over the past 100 years or so, there has been a directional shift towards increased cover of woody vegetation in drylands world-wide (Naito & Cairns 2011). This has been variously referred to as woody plant 'encroachment', 'thickening', 'invasion' and 'proliferation'. Drivers of change in grass-woody plant abundance are actively debated

*Correspondence author: E-mail: sarcher@ag.arizona.edu

and centre around changes in climate, atmospheric $[CO_2]$ and disturbance (e.g. grazing, fire) regimes (Archer, Schimel & Holland 1995; Sankaran, Ratnam & Hanan 2008; Buitenwerf *et al.* 2012). These shifts from herbaceous to woody plant dominance are widely regarded as state changes exhibiting various ecological and socio-economic threshold behaviours (Staver, Archibald & Levin 2011; D'Odorico, Okin & Bestelmeyer 2012).

Woody plant proliferation in drylands has long been of concern to managers in areas where the primary land use is cattle and sheep grazing (e.g. Fisher 1950). The proliferation of woody plants in these grazing lands typically reduces the production of valued forage grasses (Scholes & Archer 1997), while complicating animal handling and improving habitat for ectoparasites. Furthermore, and despite limited supporting evidence, woody plant encroachment has long been presumed to adversely affect stream flow and groundwater recharge. As a result, management of drylands used for cattle and sheep production has historically focused on reducing the amount of woody vegetation using a variety of technologies including mechanical treatments, herbicides, prescribed fire and biocontrol agents (Bovey 2001). Known as 'brush management' (North and South America), 'woody weed management' (Australia) and 'bush clearing' (Africa), these practices may be applied singly, in combination or sequentially, and in the context of 'integrated brush management systems' (Hamilton et al. 2004; Paynter & Flanagan 2004; Noble & Walker 2006). As a result, many regional dryland landscapes are complex mosaics of areas undergoing woody plant encroachment and areas subjected to, and transitioning from, past efforts to reduce woody cover (Asner et al. 2003; Browning & Archer 2011).

A large and growing body of work on woody plant encroachment impacts on ecosystem services has been developing (Archer 2010; Barger *et al.* 2011; Eldridge *et al.* 2011), but very little is known about how the post-encroachment management of woody vegetation influences those services. Here, we evaluate the extent to which interventions aimed at reducing the cover of proliferating woody vegetation (i) have effectively restored and subsequently sustained lost or altered ecosystem services (*sensu lato* Scholes *et al.* 2010) and (ii) are accompanied by trade-offs that might influence ecological and socio-economic decisions and priorities for dryland vegetation management.

Woody plant management and ecosystem services in grazed drylands

Drylands play an important role in global carbon, water and nitrogen cycles, and human well-being (Campbell & Stafford Smith 2000). Their extensive airsheds and watersheds provide habitat for game and non-game wildlife and a variety of ecosystem goods and services important to both local and distant settlements and cities. As such, they have considerable multidimensional value. A key component of dryland ecosystem management is maintaining the proportions of herbaceous and woody plants within a range that satisfies a given set of objectives and values, some of which may be conflicting (e.g. wildlife versus livestock, Du Toit, Kock & Deutsch 2010; Augustine *et al.* 2011).

Perspectives on woody plants in drylands vary widely depending on cultural preferences and land-use goals and objectives (Eldridge et al. 2011). In many regions of the world, woody plants are valued as a source of food (e.g. honey, fruits, seeds), fuel, charcoal, construction materials and as an important source of fodder for browsing livestock (e.g. goats, camels) and wildlife (e.g. Le Houérou 1980; Reid, Marroquín & Beyer-Münzel 1990; Reid & Ellis 1995). Additionally, there is growing recognition that woody plants on drylands can provide products with potential commercial (e.g. gums, resins) or medicinal value. However, where grazing by cattle and sheep has been the primary land use, woody plants have typically been viewed as pests. Although this view has been challenged (e.g. McKell 1977), it is pervasive and is the prevailing motivation for brush management. While this paper focuses on brush management, contrasting perspectives on the roles of woody plants provide a broader context in which to view their ecological and utilitarian importance on drylands.

This paper is biased in that it is narrowly focused on evaluating the ecological consequences of 'brush management' as it is typically applied on drylands where cattle/sheep grazing in commercial ranching or pastoral settings is the predominant land use or where management of wildlife grazers is a land-use objective (e.g. Ben-Shaher 1992; Isaacs, Somers & Dalerum 2013). Research on the consequences of this management practice has had a fairly narrow focus (Table 1). The extent to which the traditional goals associated with brush

Table 1. Proportion of brush management studies quantifying various categories of treatment effects. Published papers resulting from Web of Knowledge search strings that included 'brush management' and terms referring to specific brush management methods resulted in a database of 1350 papers that were distilled to a database of 364 papers reporting quantitative responses. These were then classified into the categories shown, where efficacy refers to the effectiveness of a brush management treatment in removing/killing target shrubs, where herbaceous/woody/faunal/soil property/water response refers to changes in ecosystem characteristics after treatment, where economics refers to studies providing monetary estimate of brush management cost-benefit and where modelling includes studies simulating responses to brush management. Papers reporting data for multiple metrics were tallied in multiple categories, but the total was not adjusted in percentage calculations. Thus, the table reflects the information reported in the literature, but not on a per-paper basis. See Appendix S1 for additional information about how the papers populating the categories in this database were generated

Category	%	Category	%
Efficacy	21	Faunal response	7
Herbaceous response		Soil properties	5
Cover/density	16	Economics	4
Production	15	Water response	3
Diversity	12	Modelling	3
Woody response	14	-	

© 2014 The Authors. Journal of Ecology © 2014 British Ecological Society, Journal of Ecology, 102, 1394–1407

1396 S. R. Archer & K. I. Predick

management have been realized (e.g. increased forage production) or the extent to which other factors (e.g. carbon sequestration, biodiversity conservation) may be affected has not been synthesized. By examining 'brush management' within the broader context of ecosystem services (Fig. 1), we aim to identify priority areas for ecological research and put this land management practice into a broader, multifaceted framework that would be a first step towards objectively evaluating suites of trade-offs associated with changes in woody plant abundance on drylands (e.g. Eldridge *et al.* 2011).

PROVISIONING SERVICE

Forage production

The cover and biomass of herbaceous vegetation valued for cattle and sheep forage typically declines as woody plant cover and basal area increase (Scholes & Archer 1997). These woody plant-driven declines in cattle and sheep carrying



Fig. 1. Potential outcomes of woody plant encroachment (WPE) and associated 'brush management' activities conducted in drylands where grazing by sheep and cattle is the primary land use. WPE variables marked with '*' have been reviewed in detail by Eldridge *et al.* (2011) and for ecosystem organic carbon by Barger *et al.* (2011). In this paper, we focus on brush management effects and provide additional information on other potential WPE effects. Symbols in boxes denote potential decreases (-), increases or improvements (+), mixed, context-dependent results $(-\setminus+)$ or insufficient information (?).

capacity have traditionally been the impetus for brush management, with the expectation that reductions in tree or shrub cover would enable the recovery of lost herbaceous production. To determine the extent to which this expectation is met, we conducted a Web of Knowledge survey of refereed journal papers using search strings that included 'brush management' and terms referring to specific brush management methods (see Appendix S1 in Supporting Information for search strings and summaries). We found that this expectation was met in 64% of the papers emerging from our search. Peak responses occurred in the 300-700 mm mean annual precipitation (MAP) range (Fig. 2). We expected the herbaceous production response would be low in the more arid climate zones, but were surprised by the poor response in high rainfall zones. Furthermore, it was not uncommon for production to remain unchanged, or even decrease, following brush management across the full spectrum of MAP. Our survey suggests the upper limit of herbaceous production responses that might be expected for a given rainfall zone.

The herbaceous production response standardized for annual rainfall varied with time since treatment (Fig. 3). The median first year response was zero (no change) and highly variable, with half of the treated sites responding positively and half negatively. By year two, the median response was slightly positive, but also highly variable. After year two, the response became more consistent and peaked in year five. The response then dropped off in years six and seven, being slightly, but consistently positive. The decline in herbaceous production with time since treatment ostensibly reflects changes in resource availability and the re-establishment of woody vegetation, either via vegetative regeneration (brush management treatments may 'top kill' the woody vegetation, but fail to cause whole-plant mortality), or from seed. Retreatment of communities is therefore necessary to maintain longterm herbaceous production and low woody plant cover.

Recognition of the need for follow-up treatments has been the basis for the development of 'integrated brush management systems' that take into account the type and timing of initial brush management actions while also considering the type and timing of follow-up treatments (Hamilton et al. 2004; Paynter & Flanagan 2004; Noble & Walker 2006). These considerations are important in assessing long-term cost-benefits (e.g. Torell, McDaniel & Ochoa 2005a). The conceptual model in Fig. 4 represents the kinds of ecological data that will be needed to evaluate the feasibility and sustainability of brush management practices from a forage production standpoint. The functions in this model will vary with climate, soils and disturbance history (e.g. McDaniel, Torell & Ochoa 2005), but the information needed to develop them is not generally available. Furthermore, there have been relatively few studies quantifying how changes in forage production actually translate into livestock production or economic benefit (Table 1).

Brush management may help balance livestock production services with other supporting and regulating services if it enables reductions in grazing pressure without forcing major herd reductions (Torell, McDaniel & Ochoa 2005a). Economic analyses suggest that returns based solely on improvements in animal performance may not be economically justified, especially when external subsidies are not available (Lee *et al.* 2001; Torell *et al.* 2005b; Tanaka, Brunson & Torell 2011). Full and explicit consideration of other ecosystem services may, however, change the cost–benefit assessment.



Fig. 2. Changes in herbaceous biomass production (kg ha⁻¹) one, two and three years after brush management as a function of current years' annual precipitation (PPT, mm) in arid and semi-arid regions (precipitation $< 1000 \text{ mm year}^{-1}$). Multiple observations for a given PPT value reflect multiple sites or different brush management methods. A data set of 1350 published papers resulting from Web of Knowledge search strings that included 'brush management' and terms referring to specific brush management methods were distilled to a database of 59 papers that directly measured changes in herbaceous production after brush management. Of those 59, 18 papers provided mean changes in production with error on both control and treatment sites. PPT was determined from nearby weather stations if not reported. The number of studies pertaining to a given brush management method is listed parenthetically in the key. Papers generating the data in the graphs are listed in Appendix S1.

© 2014 The Authors. Journal of Ecology © 2014 British Ecological Society, Journal of Ecology, 102, 1394-1407



Fig. 4. Generalized conceptual model of herbaceous response to brush management. The lag time in response $(t_1 - t_2)$, the magnitude of $(p_1 - p_2)$ and time to peak herbaceous response $(t_1 - t_3)$, the duration of peak elevated production response $(t_3 - t_4)$ and the time frame over which herbaceous productions declines as shrubs re-establish $(t_4$ onward) varies with numerous factors. Knowledge of the relationships depicted in this conceptual model for a given ecological site will help determine the type, timing and appropriate sequencing of brush management practices in an integrated brush management systems (IBMS) approach.

 t_2

Time

 t_3

 t_4

SUPPORTING SERVICES

 t_1

Primary production

A recent literature syntheses indicates above-ground NPP (woody + herbaceous) may increase, decrease or remain unchanged following woody plant encroachment (39, 42 and 19%, respectively, of the studies reviewed by Eldridge *et al.*

Fig. 3. Change in herbaceous biomass per mm of annual precipitation received after brush management. Responses are from 18 studies representing brush management with fire, herbicides and mechanical treatments (see Fig. 2 legend for details. Years 1-3 contain the same data displayed in Fig. 2). Tukey box plots show inner-quartile range (IQR; rectangle) and the median (bold line). Whiskers indicate the maximum and minimum values or the values within $1.5 \times IQR$ of the third and first quartiles, respectively. Values beyond $1.5 \times IQR$ of the 1st and 3rd quartiles were considered statistical outliers and are indicated with open circles. N = 9, 7, 4, 1, 1, 1 and 0 for years one through seven, respectively. Papers generating the data in the graph are listed in Appendix S1.

2011). North American studies suggest ANPP will decline in arid regions (mean annual precipitation, MAP < 340 mm), but increase in semi-arid and subhumid bioclimatic zones (MAP > 340 mm), with the magnitude of ANPP change increasing linearly with mean annual precipitation (Knapp *et al.* 2008; Barger *et al.* 2011). Impacts on below-ground NPP are unknown, and our knowledge of root production and turnover in dryland woody plants lags far behind that of grasses.

Although herbaceous production responses to brush management have been documented (Table 1 and Figs 2 and 3), the post-treatment responses of woody plants (Fig. 4) are largely confined to estimates of canopy cover or density. As a result, little is known about how ecosystem (herbaceous + woody) above-ground NPP changes following brush management. Hughes *et al.* (2006) quantified annual ANPP on stands recovering from brush management on clay loam sites in a 665-mm annual rainfall zone and found that above-ground woody plant C and N mass increased linearly and that ecosystem ANPP increased logarithmically after treatments. As shrubs re-established, their ANPP more than offset declines in herbaceous ANPP, resulting in a net 20% increase. Increases in biomass and ANPP also occurred on shallow clay sites, but were less pronounced.

The data discussed above suggest brush management may have neutral to positive impacts on ANPP in bioclimatic zones where woody plant productivity is comparable to, or greater than, that of the grasses they are replacing. It is also possible that in these settings, brush management activities may keep stands of encroaching woody vegetation in a relatively productive state (e.g. via promoting the replacement of older, slower-growing plants with younger, more actively growing plants and by reducing the intensity of densitydependent interactions) and thus forestall declines in ANPP that might occur at latter stages of stand development. In more arid systems where encroachment by xerophytic shrubs reduces ANPP (Knapp *et al.* 2008; Barger *et al.* 2011), ANPP recovery via brush management will depend upon the extent to which more productive mesophytic grasses can re-establish and persist (Figs 2 and 3).

Habitat and biodiversity conservation

Vascular plant richness may increase, decrease or be unaffected by woody plant encroachment (31%, 37% and 32% of studies, respectively, Eldridge *et al.* 2011). However, North American grasslands exhibit consistent (29 of 29 studies) and strong (45% on average) reductions in plant species richness with shrub encroachment, perhaps reflecting greater levels of anthropogenic disturbance (Ratajczak, Nippert & Collins 2011). In extreme cases, encroaching woody plants may form virtual plant community monocultures (Archer 2010). Brush management has the potential to reverse declines in herbaceous plant richness, but also to exacerbate it, particularly in tree-dominated drylands (Fig. 5). The herbaceous diversity response to brush management is influenced by a variety of local site factors (e.g. Kunst *et al.* 2012). In cases where herbaceous diversity was enhanced by brush management, the results were relatively short-lived (< 6 years) and on the order of those observed for biomass responses (Fig. 3).

Woody plant diversity can also be influenced by brush management. For example, in subtropical systems characterized by a diverse flora of encroaching woody plants, communities developing after brush management have lower shrub diversity and higher densities of less desirable browse species than the treated community (Fulbright & Beasom 1987; Ruthven *et al.* 1993). In systems where shrubs regenerate vegetatively, use of low intensity fire and herbicides can promote a savanna physiognomy (Ansley, Kramp & Moore 1997; Ansley, Kramp & Jones 2003) and ostensibly promote diversity.

As with plant richness, vertebrate richness may also increase, decrease or remain unchanged with woody plant encroachment (29%, 15% and 56% of studies, respectively, Eldridge *et al.* 2011). Faunal diversity response to brush

Fig. 5. Changes in herbaceous vegetation diversity following brush management. Results show ratios of values (richness, various indices) reported for paired treated and control areas. Ratios of 1.0 indicate diversity metrics on treated and control areas were similar; values < 1.0 indicate brush management decreased diversity, and values > 1.0 indicate increases in diversity. The number of studies pertaining to a given type of brush treatment is listed parenthetically in the key. Alternating grey-white panels define years. Data points are slightly displaced within years for clarity. Panel (a) shows data from non-forested drylands. Inset is a figure showing results greater than 10 years after brush management. Panel (b) shows data from self-reported forested drylands. A data set of 1350 published papers resulting from Web of Knowledge search strings that included 'brush management' and terms referring to specific brush management methods were distilled to a database of 46 papers that directly measured changes in herbaceous diversity. Of those 46, 30 papers provided mean changes in diversity (richness or Shannon diversity) with error on both control and treatment sites. Papers generating the data in the graphs are listed in Appendix S1.



© 2014 The Authors. Journal of Ecology © 2014 British Ecological Society, Journal of Ecology, 102, 1394-1407

management varies with the organisms of interest. Jones *et al.* (2000) reported that the relative total abundance and species richness of herpetofauna was similar among a variety of brush management treatments, that amphibians were most abundant in untreated and herbicide-only sites, that lizards were most abundant on untreated sites and that snakes were most abundant on sites receiving herbicide and fire. Brush management has been reported as having little influence on rodent and avian occurrence richness (Nolte & Fulbright 1997; Peterson 1997), with abundance of small mammals and herpetofauna perhaps varying more with annual rainfall than with brush management *per se* (Fulbright *et al.* 2013).

Brush management also has the potential to create conditions favourable for herbaceous weeds and invasive, nonnative species (Young, Evans & Rimby 1985; Bates, Miller & Svejcar 2007) that can adversely affect biodiversity and habitat quality. In addition, seeding operations intended to accelerate establishment of groundcover and development of a livestock forage base may be conducted in conjunction with brush management and may use non-native perennials (Hardegree et al. 2011). While this may be valued for livestock production and ground cover, these plants may represent threats to the biodiversity of native organisms (Williams & Baruch 2000; Schussman et al. 2006). Their unintended spread into areas beyond where they were planted may make it difficult to achieve goals on nearby lands. Thus, there are clear tradeoffs in habitat and biodiversity conservation that should be explicitly considered and evaluated when considering brush management options.

Historically, brush management treatments were often applied 'wall to wall'. However, treatments can be targeted for certain portions of a landscape and distributed across landscapes in both time and space, such that mosaics of vegetation structures, patch sizes, shapes and age states are created (Scifres *et al.* 1988; Fulbright 1996). This ostensibly accommodates suites of insect, reptile, mammalian and avian species with diverse habitat requirements (Jones *et al.* 2000). Thus, a low diversity shrubland or woodland developing on a grassland site can be transformed into a diverse patchwork of grassland–savanna–shrubland–woodland communities that promotes diversity at multiple scales (Fuhlendorf *et al.* 2010).

Wildlife habitat/biodiversity conservation effects of woody plant encroachment (Eldridge *et al.* 2011) and brush management (e.g. Kazmaier, Hellgren & Ruthven 2001) vary among taxa and functional groups, but as woody plant cover increases and habitat characteristics continue to shift, shrubland-/woodland-adapted species will become favoured over grassland-adapted species. Numerical richness may be maintained or enhanced if the displacement of grassland obligate species is more than offset by the arrival of new species preferring shrub or woodland habitat. However, from a physiognomic perspective, woody plant encroachment represents a net loss of grassland and savanna ecosystem types and, potentially, the plants and animals endemic to them (e.g. Bond & Parr 2010). Brush management may therefore be an important biodiversity and ecosystem conservation tool for maintaining the existence of grassland and savanna ecosystems in the face of anthropogenic land-use pressures.

REGULATING SERVICES

Carbon sequestration

The enhanced productivities accompanying woody plant encroachment in some bioclimatic zones (see '*Primary production*') can translate into increases in the above-ground carbon pool that can range from 300 to 44 000 kg C ha⁻¹ in < 60 years of woody encroachment. However, these gains will be substantially and rapidly offset by reductions in aboveground standing woody biomass that follow brush management (Asner *et al.* 2003). The net sequestration potential on a regional scale will depend on the areal extent of lands undergoing encroachment, the areal extent of lands experiencing and recovering from brush management and the rate and magnitude of woody biomass incorporation into soil organic carbon pools relative to losses associated with microbial respiration.

Changes in soil organic carbon (SOC) accompanying the conversion of grasslands to shrublands or woodlands range from positive to neutral to negative (Barger et al. 2011; Eldridge et al. 2011). Shrub-induced enhancements in SOC that have been recorded in many systems (e.g. 'fertile islands') may be an important factor underlying the pattern and extent to which herbaceous vegetation production increases following brush management. Alternatively, fluvial or aeolian nutrient translocation away from 'shrub islands' following brush management may help reinstate a more homogeneous distribution of resources by disrupting the processes that lead to the concentration of nutrients in and around shrub canopies (e.g. Ravi et al. 2009a). In these instances, the likelihood of getting grasses re-established within intershrub zones may improve (Perkins, McDaniel & Ulery 2006). Site-specific factors may dictate which of these scenarios is most likely on a given landscape.

Non-native species invading or purposely seeded following brush management could also significantly impact carbon sequestration. Alteration of wildfire regimes subsequent to the establishment of exotic annual grasses in cold deserts has the potential to offset carbon accumulations associated with woody encroachment that have occurred over the last century (Bradley *et al.* 2006) and adversely affects ecosystem services related to forage production, primary production, soil fertility and erosion (Ravi *et al.* 2009b). However, this scenario may be quite different in other drylands where highly productive, deeply rooted non-native perennial grasses have been widely planted and are spreading (Williams & Baruch 2000; Franklin *et al.* 2006; Grice 2006).

Brush management effects on SOC pools in shrubencroached grasslands have seldom been quantified. SOC of soils associated with skeletons of shrubs killed by herbicide in the 1960s was substantially lower than that of soils associated with present-day live shrubs (McClaran *et al.* 2008). Experiments at the scale of individual shrubs also indicate that losses of SOC can be substantial following removal of shrubs, but arrested and subsequently off-set if shrubs are allowed to re-establish (Klemmedson & Tiedemann 1986; Tiedemann & Klemmedson 1986; Tiedemann & Lopez 2004). Stand-level studies suggest brush management effects have neutral (Teague *et al.* 1999; Hughes *et al.* 2006) to negative (Daryanto, Eldridge & Throop 2013) impacts on SOC levels.

Grass and woody plant root biomass are concentrated in the upper soils, but the roots of woody plants typically extend to deeper depths than those of grasses (Canadell et al. 1996; Jackson et al. 1996). As such, they are likely translocating more carbon to depths where decomposition rates are lower. The effects of brush management on woody plant roots are not known. Clipping studies of shrub seedlings suggest that when above-ground portions of the plant are removed, root survival, growth and development are adversely affected (Weltzin, Archer & Heitschmidt 1998), akin to what has been widely reported for defoliated grasses. Brush management activities thus have the potential to impact root inputs into the SOC pool. The extent to which shrub coarse and fine lateral and taproots are impacted by brush management is unknown. If plants can vegetatively regenerate, impacts may be relatively small and short term, but if plants are killed, substantial amounts of carbon could enter the detrital pool with significant amounts at depths where decomposition rates are potentially very low.

Brush management modifies both the above- and belowground carbon pools, but there are few estimates of the resulting net changes over time (e.g. how gains/losses in the above-ground pool are balanced by gains/losses from the below-ground pool). Hughes *et al.* (2006), using a space-fortime substitution approach, found that above-ground biomass steadily recovered over decadal time-scales following brush management with no changes in SOC in the upper 20 cm of the soil profile. Daryanto, Eldridge & Throop (2013) found that shrub removal significantly reduced SOC pools (to 30-cm depths), but that these declines were compensated for, in part, by enhanced above-ground C accumulation derived mainly from re-establishing woody plants.

Brush management effects on carbon pools, biogeochemical cycles and herbaceous production (Figs 2-4) will vary depending on the type of soil disturbances caused, treatment efficacy and the extent to which they co-occur with other land-use practices such as livestock grazing (e.g. Ansley & Castellano 2006; Daryanto & Eldridge 2010). To further complicate matters, different brush management treatments may be applied in combination or sequentially. Treatments that minimally disturb soils (e.g. herbicide applications and prescribed burning) may have one set of effects, whereas those characterized by extensive physical disturbance to the soil surface (e.g. root plowing, grubbing, chaining) would be expected to have quite different effects. In the case of herbicide applications, woody skeletons may remain long after treatments are imposed, whereas coarse woody debris may be partially or fully combusted by prescribed burns, masticated and left on the soil surface by mechanical shredding operations, or 'pushed and stacked' into piles or windrows that may or may not be burned following chaining or cutting

operations. These various practices likely have a variety of short- and long-term direct and indirect effects on decomposition processes via their alteration of surface roughness, water infiltration and run-off, ground cover and ANPP, and by initiating large, synchronous inputs of leaf, stem and coarse woody debris onto the soil surface with widely varying degrees of contact and incorporation into the soil. Different brush management treatments will also variously influence the degree of exposure to direct sunlight and UV radiation and differentially influence soil movement via wind and water, particularly during the immediate post-treatment period when vegetation is re-establishing. These combined effects are likely to have substantial (Barnes *et al.* 2015), but largely unknown, impacts on decomposition processes.

The information reviewed above suggests that brush management effects on SOC pools, like that of woody plant encroachment, can vary in both sign and magnitude. The direction and extent of change may depend on the properties of the species or functional groups involved, the antecedent SOC status and the extent to which erosion forces are at play. Furthermore, 'brush management' is a broad catch-all for divergent classes and combinations of techniques (mechanical, chemical, pyric). Distinguishing among these is likely important. Predicting and modelling changes in soil carbon and nutrient pools following 'brush management' will likely require a better understanding of how these co-occurring factors influence biogeochemical processes and drivers.

Energy exchange and land-atmosphere interactions

Climate and atmospheric chemistry are directly and indirectly influenced by land cover via biophysical and biogeochemical aspects of land surface–atmosphere interactions (Settele *et al.* 2014). Woody plant encroachment and brush management have the potential to alter these conditions, but this has not been well studied. Increases in C and N pools that occur when woody plants proliferate in drylands may be accompanied by increases in trace gas (McCulley *et al.* 2004; Sponseller 2007; McLain, Martins & McClaran 2008) and non-methane hydrocarbons emissions (Klinger *et al.* 1998; Guenther *et al.* 1999; Geron *et al.* 2006; Jardine *et al.* 2010), but the extent to which these may be offset by brush management is unknown.

Changes in vegetation height and patchiness accompanying grass–woody plant transitions would affect boundary layer conditions and aerodynamic roughness; changes in leaf area and rooting depth would alter inputs of water vapour via transpiration; and changes in fractional ground cover, phenology and leaf habit (e.g. evergreen versus deciduous) would alter albedo and soil temperature, thus influencing evaporation and latent and sensible heat exchange. Model simulations indicate that declines in surface albedo accompanying woody plant proliferation can increase temperature and precipitation, with the amount of change increasing with increases in woody plant cover (Ge & Zou 2013). Other simulations suggest woody plant effects will vary with evergreen versus deciduous species (Beltran-Przekurat *et al.* 2008). Evidence from clearing studies suggests decreases in woody plant cover can potentially influence evapotranspiration, the incidence of convective storms and cloud formation (Jackson et al. 2007). Model simulations in tropical savannas indicate clearing of woody vegetation could increase mean surface air temperatures and wind speeds, decrease precipitation and humidity, and increase in the frequency of dry periods within the wet season (Hoffman & Jackson 2000). If brush management were to shift the composition of woody species to those that are low hydrocarbon emitters or result in the replacement of woody plant emitters with herbaceous non-emitters, it would have desirable influence on tropospheric chemistry. Thus, while information is sparse, there are indications that woody plant encroachment and brush management can influence land surface-atmosphere interactions via influences on evapotranspiration, trace gas and hydrocarbon emissions, albedo and boundary layer conditions.

Water quality and quantity

Woody plant proliferation has a variety of impacts on water resources (Huxman et al. 2005; Peters, Archer et al. 2013). It is widely believed that shrub encroachment reduces stream flow and groundwater recharge, increases erosion and surface run-off, and that brush management can reverse these trends. In cases where rigorous measurements and evaluations have been undertaken, it appears that past estimates of water savings associated with brush management may have been overestimated (Dugas, Hicks & Wright 1998; Owens & Moore 2007) and that brush management may not be achieving desired outcomes with respect to water yield (Wilcox & Thurow 2006). In systems characterized by winter rainfall, there is evidence that stream flow increases when woody cover is reduced (Hibbert 1983). However, in other semi-arid environments, the effects of shrub removal on stream flow vary depending on the traits of the woody plants, climate, soil type and geomorphology (Thurow & Hester 1997; Wilcox et al. 2006) and are not long-lasting (Sturges 1994). There may be little potential for increasing stream flow where annual precipitation is < 500 mm (Wilcox 2002; Wilcox et al. 2005).

Increased run-off and erosion are most often observed with shrub encroachment in arid systems where ground cover is sparse or where soils are prone to surface sealing (Schlesinger, Ward & Anderson 2000; Mueller, Wainwright & Parsons 2008). Although brush management has been shown to reduce erosion and increase infiltration in some drylands (Pierson *et al.* 2007), it has not done so in others (Wood, Garcia & Tromble 1991). Herbaceous ground cover, soil properties, brush management method (e.g. extent of mechanical impacts to the soil surface and patterns of woody debris distribution) strongly influence water and soil retention or loss (Hastings, Smith & Jacobs 2003; Daryanto & Eldridge 2010). As a result, broad and robust generalizations are not yet possible.

Air quality

Changes in vegetation structure accompanying woody plant encroachment alter near-surface air flow turbulence and wake interference to create conditions favouring aeolian sediment transport (Breshears *et al.* 2009). Accordingly, the conversion of grasslands to shrublands in arid bioclimatic zones with sandy soils has markedly increased levels of wind erosion and dust production in North America (Okin, Gillette & Herrick 2006; Li *et al.* 2007; l) and elsewhere (Bhattachan *et al.* 2014) with potential implications for human health (e.g. Mohamed & El Bassouni 2007). The extent to which brush management arrests or reverses dust production has not been documented, but will presumably depend upon the extent to which herbaceous ground cover can be re-established and maintained and how various brush management methods influence soil surface properties and stability.

Pests and pathogens

Human and livestock health issues related to woody plant encroachment may occur to the extent that new habitats provide microclimate, shelter or nutrient resources favouring an increase in the abundance of insects, arthropods and rodents that serve as hosts or vectors for pathogens (e.g. Hantavirus by rodents, Lyme disease by ticks). Tick-borne diseases of cattle are widespread in the world and are of significant health and economic concern (de León et al. 2012). Woody plant encroachment provides habitat more suitable to tick survival population growth than that of grasslands (Corson, Teel & Grant 2004), with woody patches on landscapes serving as sources of ticks in open patches (Teel et al. 1997). Accordingly, brush management could be a potentially important component of integrated pest/pathogen management schemes (e.g. Tatchell 1992) that could decrease the incidence and spread diseases while concurrently promoting other services.

Wildfire management

Brush management is increasingly being applied in shrubland and woodland settings to reduce fire risk or create fuel breaks (Davies *et al.* 2009). Brush management alters fuel characteristics and influences fire behaviour (Kane, Varner & Knapp 2009). However, while brush management can effectively reduce the height, mass and continuity of ladder or canopy fuels, it may also promote the production and continuity of fine surface fuels (e.g. grasses) and thus promote fire risk. Under these circumstances, livestock grazing may then come into play as a fuels management tool.

Concluding remarks

Consistent with the prevailing theory that transitions from grassland or savanna to shrubland or woodland represent ecosystem state changes, our synthesis suggests that restoration of prior states is difficult to achieve. Despite the considerable investments in personnel, equipment, fuel, chemicals, etc., associated with the application of various brush management practices, the recovery of key ecosystem services may not occur or may be short-lived and require subsequent interventions. Furthermore, brush management restorations are likely

Table 2. Ecosystem parathe consequences for landare suggested questions th	meters influenced by brush manag I management considerations. Con hat would clarify complex interrela	ement (BM) conducted in grazed ecosystems, constr straints represent priority areas for research that can tionships and trade-offs among parameters that occu	aints to predicting the extent to which BM goals related reduce uncertainty and improve predictions of the out r with management	ted to each parameter may be realized and comes of BM practices. Research inquiries
Ecosystem service	Goals	Constraints (Limited ability to predict)	Consequences (Limited ability to plan or predict)	Research inquiries
I. Forage Production	Increase production of valued forage species	Direction/magnitude of forage production response (Figs 2 and 3) Woody and herbaceous response functions (Fig. 4) Susceptibility to weed/exotic plant invasion	Timing and type of follow-up management Magnitude and duration of change in livestock production and carrying capacity	Under what management or landscape conditions do forage production increase or decrease after BM? What management practices maximize forage production after BM?
II. Above-ground Primary Production (woody + herbaceous)	Maintain or promote herbaceous ANPP for I-V	Woody plant ANPP (due to lack of information) Direction and magnitude of herbaceous ANPP response (see I)	Change in ecosystem carbon source/sink strength Outcomes of altered land surface-atmosphere interactions Trade-offs between grassland and shrubland biodiversity	What factors control woody plant ANPP? What conditions maximize post-treatment herbaceous ANPP? What conditions maximize woody plant ANPP?
III. Carbon Sequestration	Maintain or increase ecosystem carbon pools while satisfying I, II, IV and V	Changes in ANPP following BM (see I and II) Response of shrub roots (shallow, deep) to BM treatments Impacts of contrasting BM methods on above- ground detrial pool Response of mineral soil organic carbon pool to BM treatments Non-methane hydrocarbon emissions of woody species	Change in ecosystem carbon sink strength Altered land surface-atmosphere interaction potential	What are the short-and long-term effects of BM on carbon sequestration? Under what conditions is carbon sequestration maximized in grasslands? In shrublands?
IV. Biodiversity	Maintain or recover habitat for grassland flora and fauna	Woody cover threshold at which adverse effects begin Herbaceous response (Fig. 5) Faunal response due to high variation among functional groups and with extent and spatial arrangement of BM treatments Microbial community response	Loss of grassland obligate species Consequences of altered structure/function processes in grassland/savanna systems Timing/type/placement of initial and follow-up BM	How does BM affect grassland biodiversity and habitat? Shrubland biodiversity and habitat? What are biodiversity trade-offs that occur with BM?
V. Water Quality and Quantity	Reduce erosion and sedimentation Increase stream flow Increase groundwater recharge	Ground cover response (see I) which affects surface erosion and hydrology Influence of annual precipitation amount and seasonality Potential effects because of variation among sites in soils, geomorphology and woody species traits	Erosion without a positive ground cover response Effects on local hydrology owing to paucity of watershed-scale assessments for comparison and importance of site-scale drive	What are watershed versus regional scale benefits of BM to water quality and quantity?

1 each related to olect RM , 4-1-1-1 4 ÷ -ţ 4 (BM) 4 4 2 ġ Щ 2 qld

hysteretic, occurring through different pathways than those generating the initial state change and reflecting altered functional interactions between soils, plants animals and the atmosphere.

Drylands prone to woody plant proliferation present a novel series of dilemmas, challenges and opportunities for mitigation. For example, the fact that woody plant proliferation can promote ecosystem primary production and carbon sequestration under some circumstances may trigger new land-use drivers for biofuel production (Park et al. 2012) or as industries seek opportunities to offset CO₂ emissions. Woody plant proliferation in grasslands and savannas traditionally managed for cattle and sheep grazing may therefore shift from being an economic liability to a source of income and economic diversification. However, under this scenario, grasslands and savannas and the plants and animals endemic to them would be at risk and hydrology, tropospheric chemistry and meteorology altered. At present, our ability to evaluate and weigh these trade-offs, and their potentially synergistic interactions. is limited owing to variable and often conflicting results or to a paucity of information (Table 2). These ecosystem science challenges are magnified when placed in the human dimension context of cultural traditions, stakeholder preferences and priorities, market externalities and climate change.

Sustainability has ecological, social and economic components, and woody plant encroachment into drylands affects all three. Where the prevailing land use is cattle and sheep grazing, land managers often seek to reduce woody plant cover as a means of maintaining or promoting livestock production. Within this context, the scientific community is challenged with ascertaining the settings and conditions under which grass-to-woody state transitions are most likely to occur, the spatial location and point(s) in time at which interventions might be most likely to achieve the outcomes desired for a given set of management or policy goals, and the combination and time-series of intervention methods that are most likely to effect desired changes within socio-economic constraints. However, the management of woody-herbaceous mixtures extends well beyond the traditional concerns of livestock production to include potential effects on a variety of other ecosystem services (Fig. 1). The scientific community is challenged with quantifying and monitoring the concomitant impacts of woody plant encroachment and brush management so that trade-offs (e.g. Nelson et al. 2009) can be objectively

	Ecosystem states			[Management priorities			
	S.		Biophysical, Ecological, Economic and Social Drivers of Brush Management					
	Grassland/savanna				Livestock grazing	Water conservation	Grassland conservation	Recreation
	Shrub encroachment	Response variables		Priority Rankings				
es		/	0	stocking rate	1	3	3	3
bu	<i>S</i> ₁		5 S	treatment cost	1	2	2	2
ite chai	shrub-encroached grassland		i S Ci	recreation income	3	3	2	1
		ec v	forage production	1	1	3	3	
sta				air quality	3	3	2	2
E	Brush treatment	\setminus	a	biodiversity	3	3	1	1
ste			<u>.</u>	C sequestration	3	3	2	3
S	S.		N S	soil erosion	2	1	1	2
N N	Restored grassland/savanna		N.	water quality & quantity	2	1	1	2
			primary production	1	2	2	3	
				fire (wild/preseribed)	2	2	2	2
	Monitoring s _n	Site	nie (wild/prescribed)	2	2	2	2	
			land use history	2	2	2	2	
			ahrub troito	2	2	2	2	
\sim	Managed grassland/savanna			sillub traits	2	2	2	2
				types of recreation	3	3	2	· · ·
		- 1						
	Integrated brush management	t systen	า					

Fig. 6. A conceptual framework showing ecosystem state transitions associated with shrub encroachment and subsequent brush management (BM). Management and ecological drivers interact to transition land parcels among ecosystem states (s_n) over time (white arrows). The impetus to prescribe BM treatments in grazed drylands is most often motivated by concerns about livestock grazing, water conservation, grassland conservation or recreation that constitute classes of 'drivers' (columns in the expanded management priorities box). The relative importance of these drivers will vary with values and land-use objectives (e.g. livestock grazing may be primary driver in some circumstances; grassland conservation the primary driver in other circumstances; where 'multiple use' is a mandate, a balance among drivers would be needed). Examples of classes of socio-economic, ecological, and site response variables relevant to the decision to implement BM treatments are listed (rows in expanded management priorities box). In a given s_n , each response variable would be assigned a priority ranking for a given BM driver (in this example, '1', '2', '3' for primary, secondary, tertiary). The performance of response variables would be monitored in an adaptive management context within that state (black arrows) to either maintain it or promote its transition to an alternate state better aligned to management priorities. As environmental conditions, management goals or ecosystem states change, priority rankings among drivers (columns) and response variables (rows) would then be revised. This framework would be embedded within an integrated brush management systems context (grey box, Scifres 1987; Paynter & Flanagan 2004; Noble & Walker 2006; Kunst *et al.* 2012; Sheley *et al.* 2010). The science community is challenged with providing the information needed to quantify response variables such that weighting factors and rankings can be developed and trade-offs evaluated (e.g. Fig. 1 and Table 2).

evaluated at spatial and temporal scales relevant to land management and policy. Eldridge *et al.* (2011) present a framework for characterizing and evaluating the diverse array of woody plant encroachment effects based on human use preferences, woody plant traits and abiotic contingencies. An important next step would be to place 'brush management' effects within this framework, so as to provide a comprehensive perspective on the environmental consequences of changes in woody plant abundance – decreases as well as increases – on drylands (Fig. 6). Elaboration of this framework will position the management community to devise approaches for creating or maintaining woody–herbaceous mixtures in arrangements that satisfy competing land-use and conservation objectives and to identify and objectively define best management practices within constraints imposed by climate and soils.

Acknowledgements

This work was supported, in part, by the US National Science Foundation DEB-1413900, DEB-1242747 and DEB-0816162, the South America Resilience and Sustainability Studies Institute (SARAS²), the Arizona Agricultural Experiment Station and benefitted from interactions with K. Davies, T. Fulbright, K. McDaniel and B. Wilcox via the US Department of Agriculture/Natural Resources Conservation Service Rangeland Conservation Effects Assessment Program.

Data Accessibility

Data presented in Figs 2, 3 and 5 were obtained from published, peer-reviewed papers obtained from *Web of Knowledge*. A list of these papers and the figures that utilize their data are provided in Appendix S1. Raw data are available from the Dryad Digital Repository (Archer & Predick 2014).

References

- Ansley, R.J. & Castellano, M.J. (2006) Strategies for savanna restoration in the southern Great Plains: effects of fire and herbicides. *Restoration Ecology*, 14, 420–428.
- Ansley, R.J., Kramp, B.A. & Jones, D.L. (2003) Converting mesquite thickets to savanna through foliage modification with clopyralid. *Journal of Range Management*, 56, 72–80.
- Ansley, R.J., Kramp, B.A. & Moore, T.R. (1997) Development and management of mesquite savanna using low intensity prescribed fires. *Proceedings – Fire Effects on Rare and Endangered Species and Habitats Conference* (ed. J. Greenlee), pp. 155–161. International Association of Wildland Fire, Coeur d' Alene, Idaho.
- Archer, S. (2010) Rangeland conservation and shrub encroachment: new perspectives on an old problem. Wild Rangelands: Conserving Wildlife While Maintaining Livestock in Semi-Arid Ecosystems (eds J. du Toit, R. Kock & J. Deutsch), pp. 53–97. Wiley-Blackwell Publishing, Oxford, UK.
- Archer, S. R. & Predick, K. I. (2014) Data from: An ecosystem services perspective on brush management: research priorities for competing land-use objectives. *Dryad Digital Repository*, doi:10.5061/dryad.85223.
- Archer, S., Schimel, D.S. & Holland, E.A. (1995) Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*, **29**, 91–99.
- Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J. & Wessman, C.A. (2003) Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. *Global Change Biology*, 9, 316–335.
- Augustine, D.J., Veblen, K.E., Goheen, J.R., Riginos, C. & Young, T.P. (2011) Pathways for positive cattle-wildlife interactions in semiarid rangelands. *Smithsonian Contributions to Zoology*, **632**, 55–71.
- Barger, N.N., Archer, S., Campbell, J., Huang, C., Morton, J. & Knapp, A. (2011) Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research – Biogeosciences*, **116**, G00K07.
- Barnes, P., Throop, H., Archer, S., Breshears, D., McCulley, R. & Tobler, M. (2015) Sunlight and soil-litter mixing: dual drivers of litter decomposition in drylands. *Progress in Botany*, **76**, 273–302.

- Bates, J.D., Miller, R.E. & Svejcar, T. (2007) Long-term vegetation dynamics in a cut western juniper woodland. Western North American Naturalist, 67, 549–561.
- Beltran-Przekurat, A., Pielke, R.A. Sr, Peters, D.P.C., Snyder, K.A. & Rango, A. (2008) Modeling the effects of historical vegetation change on near-surface atmosphere in the northern Chihuahuan Desert. *Journal of Arid Environments*, **72**, 1897–1910.
- Ben-Shaher, R. (1992) The effects of bush clearance on African ungulates in a semi-arid nature reserve. *Ecological Applications*, 2, 95–101.
- Bhattachan, A., D'Odorico, P., Dintwe, K., Okin, G.S. & Collins, S.L. (2014) Resilience and recovery potential of duneland vegetation in the southern Kalahari. *Ecosphere*, 5, 2–14.
- Bond, W.J., Midgley, G.F. & Woodward, F.T. (2003) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biology*, 9, 973–982.
- Bond, W.J. & Parr, C.L. (2010) Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biological Conservation*, 143, 2395– 2404.
- Bovey, R.W. (2001) Woody Plants and Woody Plant Management: Ecology, Safety, and Environmental Impact. Marcel Dekker Inc, New York.
- Bradley, B.A., Houghtonw, R.A., Mustard, J.F. & Hamburg, S.P. (2006) Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology*, **12**, 1815–1822.
- Breshears, D.D., Whicker, J.J., Zou, C.B., Field, J.P. & Allen, C.D. (2009) A conceptual framework for dryland aeolian sediment transport along the grassland-forest continuum: effects of woody plant canopy cover and disturbance. *Geomorphology*, **105**, 28–38.
- Browning, D. & Archer, S. (2011) Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. *Ecologi*cal Applications, **21**, 1649–1622.
- Buitenwerf, R., Bond, W.J., Stevens, N. & Trollope, W.S.W. (2012) Increased tree densities in South African savannas: > 50 years of data suggests CO₂ as a driver. *Global Change Biology*, **18**, 675–684.
- Campbell, B.D. & Stafford Smith, D.M. (2000) A synthesis of recent global change research on pasture and range production: reduced uncertainties and their management implications. *Agriculture, Ecosystems and the Environment*, 82, 39–55.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia*, **108**, 583–595.
- Corson, M.S., Teel, P.D. & Grant, W.E. (2004) Microclimate influence in a physiological model of cattle-fever tick (*Boophilus* spp.) population dynamics. *Ecological Modelling*, **180**, 487–514.
- Daryanto, S. & Eldridge, D.J. (2010) Plant and soil surface responses to a combination of shrub removal and grazing in a shrub-encroached woodland. *Journal of Environmental Management*, **91**, 2639–2648.
- Daryanto, S., Eldridge, D.J. & Throop, H.L. (2013) Managing semi-arid woodlands for carbon storage: grazing and shrub effects on above- and belowground carbon. Agriculture, Ecosystems & Environment, 169, 1–11.
- Davies, K.W., Bates, J.D., Johnson, D.D. & Nafus, A.M. (2009) Influence of mowing Artemisia tridentata ssp. wyomingensis on winter habitat for wildlife. Environmental Management, 44, 84–92.
- D'Odorico, P., Okin, G.S. & Bestelmeyer, B.T. (2012) A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrolo*gy, 5, 520–530.
- Du Toit, J., Kock, R. & Deutsch, J. (2010) Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems. *Conservation Science & Practice Series 6* (eds J. du Toit, R. Kock & J. Deutsch), pp. 448. Blackwell Publishing Ltd, Oxford, UK.
- Dugas, W.A., Hicks, R.A. & Wright, P. (1998) Effect of removal of Juniperus ashei on evapotranspiration and runoff in the Seco Creek watershed. *Water Resources Research*, 34, 1499–1506.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, 14, 709–722.
- Fisher, C.E. (1950) The mesquite problem in the Southwest. Journal of Range Management, 3, 60–70.
- Franklin, K.A., Lyons, K., Nagler, P.L., Lampkin, D., Glenn, E.P., Molina-Freaner, F., Markow, T. & Huete, A.R. (2006) Buffelgrass (*Pennisetum ciliare*) land conversion and productivity in the plains of Sonora, Mexico. *Biological Conservation*, **172**, 62–71.
- Fuhlendorf, S.D., Townsend, D.E., Elmore, R.D. & Engle, D.M. (2010) Pyricherbivory to promote rangeland heterogeneity: evidence from small mammal communities. *Rangeland Ecology & Management*, 63, 670–678.

© 2014 The Authors. Journal of Ecology © 2014 British Ecological Society, Journal of Ecology, 102, 1394–1407

1406 S. R. Archer & K. I. Predick

- Fulbright, T.E. (1996) Viewpoint a theoretical basis for planning woody plant control to maintain species diversity. *Journal of Range Management*, 49, 554–559.
- Fulbright, T.E. & Beasom, S.L. (1987) Long-term effects of mechanical treatment on white-tailed deer browse. Wildlife Society Bulletin, 15, 560–564.
- Fulbright, T.E., Lozano-Cavazos, E.A., Ruthven, D.C. & Litt, A.R. (2013) Plant and small vertebrate composition and diversity 36–39 years after root plowing. *Rangeland Ecology & Management*, **66**, 19–25.
- Ge, J. & Zou, C. (2013) Impacts of woody plant encroachment on regional climate in the southern Great Plains of the United States. *Journal of Geophysi*cal Research: Atmospheres, **118**, 9093–9104.
- Geron, C., Guenther, A., Greenberg, J., Karl, T. & Rasmussen, R. (2006) Biogenic volatile organic compound emissions from desert vegetation of the southwestern US. *Atmospheric Environment*, **40**, 165–1660.
- Grice, A.C. (2006) The impacts of invasive plant species on the biodiversity of Australian rangelands. *The Rangeland Journal*, **28**, 1–27.
- Guenther, A., Archer, S., Greenberg, J., Harley, P., Helmig, D., Klinger, L., Vierling, L., Wildermuth, M., Zimmerman, P. & Zitzer, S. (1999) Biogenic hydrocarbon emissions and landcover/climate change in a subtropical savanna. *Physics and Chemistry of the Earth (B)*, 24, 659–667.
- Hamilton, W.T., McGinty, A., Ueckert, D.N., Hanselka, C.W. & Lee, M.R. (2004) Brush Management: Past, Present, Future. A&M University Press, College Station, TX, USA.
- Hardegree, S.P., Jones, T.A., Roundy, B.A., Shaw, N.L. & Monaco, T.L. (2011) An assessment of range planting as a conservation practice. *Conservation Benefits of Rangeland Practices: Assessment, Recommendations, and Knowledge Gaps* (ed. D. Briske), pp. 171–212. United States Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.
- Hastings, B.K., Smith, F.M. & Jacobs, B.F. (2003) Rapidly eroding pinon-juniper woodlands in New Mexico: response to slash treatment. *Journal of Envi*ronmental Quality, **32**, 1290–1298.
- Hibbert, A.R. (1983) Water yield improvement potential by vegetation management on western rangelands. *Water Resources Bulletin*, 19, 375–381.
- Hoffman, W.A. & Jackson, R.B. (2000) Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. *Journal of Climate*, 13, 1593–1602.
- Hughes, R.F., Archer, S.R., Asner, G.P., Wessman, C.A., McMurtry, C., Nelson, J. & Ansley, R.J. (2006) Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. *Global Change Biology*, **12**, 1733–1747.
- Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T. & Jackson, R.B. (2005) Ecohydrological implications of woody plant encroachment. *Ecology*, **86**, 308–319.
- Isaacs, L., Somers, M. & Dalerum, F. (2013) Effects of prescribed burning and mechanical bush clearing on ungulate space use in an African savannah. *Restoration Ecology*, 21, 260–266.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.
- Jackson, R., Farley, K., Hoffmann, W., Jobbágy, E. & McCulley, R. (2007) Carbon and water tradeoffs in conversions to forests and shrublands. *Terrestrial Ecosystems in a Changing World* (eds J. Canadell, D. Pataki & L. Pitelka), pp. 237–246. Springer, Berlin Heidelberg.
- Jardine, K., Abrell, L., Kurc, S.A., Huxman, T., Ortega, J. & Guenther, A. (2010) Volatile organic compound emissions from *Larrea tridentata* (creosote bush). *Atmospheric Chemistry and Physics*, **20**, 12191–12206.
- Jones, B., Fox, S.F., Leslie, D.M., Engle, D.M. & Lochmiller, R.L. (2000) Herpetofaunal responses to brush management with herbicide and fire. *Journal* of Range Management, 53, 154–158.
- Kane, J.M., Varner, J.M. & Knapp, E.E. (2009) Novel fuelbed characteristics associated with mechanical mastication treatments in northern California and south-western Oregon, USA. *International Journal of Wildland Fire*, 18, 686–697.
- Kazmaier, R., Hellgren, E. & Ruthven, D. (2001) Habitat selection by the Texas tortoise in a managed thornscrub ecosystem. *Journal of Wildlife Man*agement, 65, 653–660.
- Klemmedson, J.O. & Tiedemann, A.R. (1986) Long-term effects of mesquite removal on soil characteristics: II. Nutrient Availability. *Soil Science Society* of America Journal, **50**, 476–480.
- Klinger, L., Greenberg, J., Guenther, A., Tyndall, G., Zimmerman, P., Bangui, M., Moutsambote, J.M. & Kenfack, D. (1998) Patterns in volatile organic compound emissions along a savanna-rainforest gradient in Central Africa. *Journal of Geophysical Research*, **102**, 1443–1454.
- Knapp, A., Briggs, J., Collins, S., Archer, S., Bret-Harte, M., Ewers, B., Peters, D., Young, D., Shaver, G., Pendall, E. & Cleary, M. (2008) Shrub encroach-

ment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, **14**, 615–623.

- Kunst, C., Ledesma, R., Bravo, S., Albanesi, A., Anriquez, A., van Meer, H. & Godoy, J. (2012) Disrupting woody steady states in the Chaco region (Argentina): responses to combined disturbance treatments. *Ecological Engineering*, **42**, 42–53.
- Le Houérou, H.N. (1980) Browse in Africa: The Current State of Knowledge, pp. 491. International Livestock Center for Africa, Addis Abba, Ethiopia.
- Lee, A.C., Conner, J.R., Mjelde, J.W., Richardson, J.W. & Stuth, J.W. (2001) Regional cost share necessary for rancher participation in brush control. *Journal of Agricultural and Resource Economics*, **26**, 478–490.
- de León, A.A.P., Teel, P.D., Auclair, A.N., Messenger, M.T., Guerrero, F.D., Schuster, G. & Miller, R.J. (2012) Integrated strategy for sustainable cattle fever tick eradication in USA is required to mitigate the impact of global change. *Frontiers in Physiology*, 3, 1–17.
- Li, J., Okin, G.S., Alvarez, L. & Epstein, H. (2007) Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. *Biogeochemistry*, 85, 317–332.
- McClaran, M.P., Moore-Kucera, J., Martens, D.A., van Haren, J. & Marsh, S.E. (2008) Soil carbon and nitrogen in relation to shrub size and death in a semi-arid grassland. *Geoderma*, 145, 60–68.
- McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M. & Zuberer, D.A. (2004) Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology*, 85, 2804–2817.
- McDaniel, K.C., Torell, L.A. & Ochoa, C.G. (2005) Wyoming big sagebrush recovery and understory response with tebuthiuron control. *Rangeland Ecol*ogy & Management, 58, 65–76.
- McKell, C.M. (1977) Arid land shrubs: a neglected resource. Agricultural Mechanization in Asia, Winter, 28–36.
- McLain, J.E.T., Martins, D.A. & McClaran, M.P. (2008) Soil cycling of trace gases in response to mesquite management in a semiarid grassland. *Journal* of Arid Environments, **72**, 1654–1665.
- Mohamed, A.-M. & El Bassouni, K. (2007) Externalities of fugitive dust. *Environmental Monitoring and Assessment*, 130, 83–98.
- Mueller, E.N., Wainwright, J. & Parsons, A.J. (2008) Spatial variability of soil and nutrient characteristics of semi-arid grasslands and shrublands, Jornada Basin, New Mexico. *Ecohydrology*, 1, 3–12.
- Naito, A.T. & Cairns, D.M. (2011) Patterns and processes of global shrub expansion. *Progress in Physical Geography*, 35, 423–442.
- Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D. et al. (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment, 7, 4–11.
- Noble, J.C. & Walker, P. (2006) Integrated shrub management in semi-arid woodlands of eastern Australia: a systems-based decision support system. *Agricultural Systems*, 88, 332–359.
- Nolte, K.R. & Fulbright, T.E. (1997) Plant, small mammal, and avian diversity following control of honey mesquite. *Journal of Range Management*, 50, 205–212.
- Okin, G.S., Gillette, D.A. & Herrick, J.E. (2006) Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *Journal of Arid Environments*, 65, 253–275.
- Owens, M.K. & Moore, G.W. (2007) Saltcedar water use: realistic and unrealistic expectations. *Rangeland Ecology and Management*, **60**, 553–557.
- Park, S.C., Ansley, R.J., Mirik, M. & Maindrault, M.A. (2012) Delivered biomass costs of honey mesquite (*Prosopis glandulosa*) for bioenergy uses in the south central USA. *Bioenergy Research*, 5, 989–1001.
- Paynter, Q. & Flanagan, G.J. (2004) Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, Mimosa pigra. *Journal of Applied Ecology*, **41**, 615–629.
- Perkins, S.R., McDaniel, K.C. & Ulery, A.L. (2006) Vegetation and soil change following creosote bush (*Larrea tridentata*) control in the Chihuahuan Desert. *Journal of Arid Environments*, 64, 152–173.
- Peters, D.P.C., Archer, S.R., Brooks, M.L., Brown, J., Monger, H.C. & Goldstein, J.H. *et al.* (2013) Vulnerability of ecosystem services to cumulative threats that result in desertification. *Ecosystem Functions and Services: Volume 5* (eds T. Seastedt & K. Suding), pp. 239–258. Elsevier, Amsterdam.
- Peterson, R. (1997) Comment: plant, small mammal, and avian diversity following control of honey mesquite. *Journal of Range Management*, 50, 443–443.
- Pierson, F.B., Bates, J.D., Svejcar, T.J. & Hardegree, S.P. (2007) Runoff and erosion after cutting western juniper. *Rangeland Ecology & Management*, 60, 285–292.

- Ratajczak, Z., Nippert, J.B. & Collins, S.L. (2011) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, 93, 697–703.
- Ravi, S., D'Odorico, P., Wang, L., White, C., Okin, G., Macko, S. & Collins, S. (2009a) Post-fire resource redistribution in desert grasslands: a possible negative feedback on land degradation. *Ecosystems*, **12**, 434–444.
- Ravi, S., D'Odorico, P., Collins, S.L. & Huxman, T.E. (2009b) Can biological invasions induce desertification? *New Phytologist*, 181, 512–515.
- Reid, R.S. & Ellis, J.E. (1995) Impacts of pastoralists on woodlands in South Turkana, Kenya: livestock-mediated tree recruitment. *Ecological Applications*, 5, 978–992.
- Reid, N., Marroquín, J. & Beyer-Münzel, P. (1990) Utilization of shrubs and trees for browse, fuelwood and timber in Tamaulipan thornscrub, northeastern Mexico. *Forest Ecology and Management*, **36**, 61–79.
- Ruthven, D.C.I., Fulbright, T.E., Beasom, S.L. & Hellgren, E.C. (1993) Longterm effects of root plowing on vegetation in the eastern south Texas plains. *Journal of Range Management*, 46, 351–354.
- Sankaran, M., Ratnam, J. & Hanan, N. (2008) Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, **17**, 236–245.
- Schlesinger, W.H., Ward, T.J. & Anderson, J. (2000) Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. Field plots. *Biogeochemistry*, **49**, 69–86.
- Scholes, R. & Archer, S. (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics, 28, 517–544.
- Scholes, R., Biggs, R., Palm, C. & Duraiappah, A. (2010) Assessing state and trends in ecosystem services and human well-being. *Ecosystems and Human Well-Being: A Manual for Assessment Practitioners* (eds N. Ash, H. Blanco, C. Broan, K. Garcia, T. Tomich, B. Vira & M. Zurek), pp. 115–150. Island Press, Washington, DC, USA.
- Schussman, H.R., Geiger, E.L., Mau-Crimmins, T.M. & Ward, J. (2006) Spread and current potential distribution of an alien grass, Eragrostis lehmanniana Nees, in the southwestern USA: comparing historical data and ecological niche models. *Diversity and Distributions*, **12**, 582–592.
- Scifres, C.J. (1987) Decision-analysis approach to brush management planning: ramifications for integrated range resources management. *Journal of Range Management*, 40, 482–490.
- Scifres, C.J., Hamilton, W.T., Koerth, B.H., Flinn, R.C. & Crane, R.A. (1988) Bionomics of patterned herbicide application for wildlife habitat enhancement. *Journal of Range Management*, **41**, 317–321.
- Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T. & Taboada, M.A. (2014) Terrestrial and inland water systems. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White), pp. 1–32. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Sheley, R., James, J., Smith, B. & Vasquez, E. (2010) Applying ecologically based invasive-plant management. *Rangeland Ecology & Management*, 63, 605–613.
- Sponseller, R.C. (2007) Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Global Change Biology*, 13, 426–436.
- Staver, A.C., Archibald, S. & Levin, S.A. (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science*, 334, 230–232.
- Sturges, D.L. (1994) High-elevation watershed response to sagebrush control in south-central Wyoming. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Research Paper, 1–18.
- Tanaka, J., Brunson, M. & Torell, L. (2011) A social and economic assessment of rangeland conservation practices. *Conservation Benefits of Rangeland Practices: Assessment, Recommendations, and Knowledge Gaps* (ed. D. Briske),

pp. 371–422. United States Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.

- Tatchell, R.J. (1992) Ecology in relation to integrated tick management. International Journal of Tropical Insect Science, 13, 551–561.
- Teague, W., Foy, J., Cross, B. & Dowhower, S. (1999) Soil carbon and nitrogen changes following root-plowing of rangeland. *Journal of Range Management*, 52, 666–670.
- Teel, P.D., Marin, S., Grant, W.E. & Stuth, J.W. (1997) Simulation of host-parasite-landscape interactions – influence of season and habitat on cattle fever tick (Boophilus sp.) population dynamics in rotational grazing systems. *Ecological Modelling*, 97, 87–97.
- Thurow, T.L. & Hester, J.W. (1997) How an Increase or reduction in juniper cover alters rangeland hydrology. Juniper Symposium Proceedings: Texas Agricultural Experiment Station Technical Report, pp. 4–9, C4–21. Texas A & M Agricultural Experiment Station, College Station, TX, USA.
- Tiedemann, A.R. & Klemmedson, J.O. (1986) Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. *Soil Science Society of America Journal*, **50**, 472–475.
- Tiedemann, A.R. & Lopez, C.F. (2004) Assessing soils factors in wildland improvement programs. *Restoring Western Ranges and Wildlands*, Vol. 1 (eds S.B. Monsen, R. Stevens & N.L. Shaw), pp. 39–64. USDA Forest Service, Rocky Mountain Research Station Gen Tech Rep RMRS-GTR-136-vol-1, Ft. Collins, CO, USA.
- Torell, L.A., McDaniel, K.C. & Ochoa, C.G. (2005a) Economics and optimal frequency of Wyoming big sagebrush control with tebuthiuron. *Rangeland Ecology & Management*, 1, 77–84.
- Torell, L.A., Rimbey, N.R., Ramirez, O.A. & McCollum, D.W. (2005b) Income earning potential versus consumptive amenities in determining ranchland values. *Journal of Agricultural and Resource Economics*, **30**, 537–560.
- Weltzin, J.F., Archer, S.R. & Heitschmidt, R.K. (1998) Defoliation and woody plant (*Prosopis glandulosa*) seedling regeneration: potential vs realized herbivory tolerance. *Plant Ecology*, **138**, 127–135.
- Wilcox, B.P. (2002) Shrub control and streamflow on rangelands: a process based viewpoint. *Journal of Range Management*, 55, 318–326.
- Wilcox, B.P. & Thurow, T.L. (2006) Emerging issues in rangeland ecohydrology: vegetation change and the water cycle. *Rangeland Ecology & Management*, **59**, 220–224.
- Wilcox, B.P., Owens, M.K., Knight, R.W. & Lyons, R.K. (2005) Do woody plants affect streamflow on semiarid karst rangelands? *Ecological Applications*, **151**, 127–136.
- Wilcox, B.P., Owens, M.K., Dugas, W.A., Ueckert, D.N. & Hart, C.R. (2006) Shrubs, streamflow, and the paradox of scale. *Hydrological Processes*, 20, 3245–3259.
- Williams, D.G. & Baruch, Z. (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions*, 2, 123–140.
- Wood, M.K., Garcia, E.L. & Tromble, J.M. (1991) Runoff and erosion following mechanical and chemical control of creosote bush (*Larrea tridentata*). *Weed Technology*, 5, 48–53.
- Young, J., Evans, R. & Rimby, C. (1985) Weed control and revegetation following western juniper control. Weed Science, 33, 513–517.

Received 23 January 2014; accepted 7 August 2014 Handling Editor: Fernando Maestre

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data collection techniques and references utilized in Table 1 and Figs 2, 3 and 5.